Recovery of Claw Size and Function Following Autotomy in *Cancer productus* (Decapoda: Brachyura)

RACHEL E. BROCK[1] AND L. DAVID SMITH[2,*]

Department of Zoology, University of Alberta, Edmonton, Alberta T6G 2E9, and Bamfield Marine Station, Bamfield, British Columbia VOR 1B0, Canada

Abstract. We examined recovery of claw size and function following autotomy in red rock crabs *Cancer productus*. We also tested for costs of regeneration to growth and documented the frequency of claw injury in *C. productus* populations in Barkley Sound, Canada. Field and laboratory results indicated that crabs required at least three molts to recover a full-length cheliped. For injured crabs, regenerating claws were significantly less powerful than contralateral, normal (*i.e.*, uninjured) claws even two instars after autotomy. Greater mechanical advantage in normal claws of injured (*versus* uninjured) crabs, however, suggests some morphological response by the remaining normal claw to increased exercise. Despite this compensatory response, our experiments indicate that injured crabs remain at a significant disadvantage while foraging. After adjusting for differences in propodus length, both regenerating and normal claws of injured crabs delivered significantly lower crushing forces than did claws of intact crabs. Energetic costs, in the form of reduced body size increase at the molt, were detected only for crabs regenerating both claws. High incidences of single claw loss in *C. productus* in Barkley Sound, together with our experimental data, suggest that much of the population experiences a prolonged foraging handicap following injury.

Introduction

Many animals possess the ability to self-amputate, or autotomize, an appendage in response to injury or its threat (Robinson *et al.*, 1970; Medel *et al.*, 1988; McCallum *et al.*, 1989; Smith, 1995). Although the absence of an appendage can impair subsequent performance (*e.g.*, Vitt *et al.*, 1977; Sekkelsten, 1988; Smith and Hines, 1991a; Davenport *et al.*, 1992; Smith, 1992, 1995; Juanes and Smith, 1995), the handicap is considered temporary because, in most cases, individuals are able to regenerate the missing structure. Regeneration of a normal-length limb generally requires a minimum of two molts (*e.g.*, Miller and Watson, 1976; Savage and Sullivan, 1978; Smith, 1990); however, the actual time to replace an appendage completely can vary dramatically (*e.g.*, <1 y in juvenile king crabs, *Paralithodes camtschatica*, 4–7 y in young adults; Edwards, 1972). If the regenerative process is prolonged and the regenerating appendage functions at a level significantly below that of a normal one, then the long-term cost of autotomy to individual performance could be high. In this study, we examine recovery of claw size and function following autotomy in *Cancer productus*, a common shallow-water molluscivorous crab in the eastern Pacific Ocean.

In crustaceans, recovery of a normal-length limb following autotomy is dependent on the molt frequency and the proportion of limb length replaced at each ecdysis (Goss, 1969; Skinner, 1985). These factors, in turn, can vary with species, age of the animal, and extent of injury. For example, blue crabs (*Callinectes sapidus*) are able to recover 85% to 90% of their normal limb length in the first post-autotomy molt and nearly 100% in the second molt (Smith, 1990). In contrast, spider crabs (*Chionoecetes opilio*) recover about 48% and 73% of the normal

limb length in the first and second molt (Miller and Watson, 1976). Because molting frequency typically declines with age in most crustaceans (Hartnoll, 1982), regeneration will take longer in older individuals (Smith and Hines, 1991b). The effect of limb autotomy on the molt cycle is more complex; it can accelerate or delay ecdysis, depending on the number of limbs removed and the stage at which injury occurs (Hopkins, 1982; Spivak, 1990; Smith, 1990).

In many brachyuran crab populations, cheliped (claw) autotomy is the most common form of limb injury (Smith and Hines, 1991b; Juanes and Smith, 1995). This type of injury can have profound fitness consequences given the functional importance of chelipeds (e.g., Lee and Seed, 1992; Lee, 1995; Seed and Hughes, 1995) and their relative contribution to total body mass (e.g., ca. 50% in *Menippe mercenaria*, Simonson and Steele, 1981). In molluscivorous crabs, chelipeds must generate sufficient closing force to break the defensive armor of their prey (Vermeij, 1983; Boulding and LaBarbara, 1986). Because closing force is a function of muscle mass as well as the size, dentition, and leverage properties (e.g., mechanical advantage) of the claw (Brown et al., 1979; Elner and Campbell, 1981), one would expect the smaller regenerating claw to deliver less crushing force than a contralateral limb of normal size. Regenerating claws, however, might also fail to operate at their size-specific functional capacity if their leverage properties or muscle development differ from those of equivalently sized, normal chelipeds. In either case, smaller closing forces generated by regenerating chelipeds could limit the type or size of prey taken (Elner, 1980).

The potential exists for the contralateral normal cheliped to compensate for reduced function in the regenerating cheliped through either behavioral or morphological changes. Smith and Palmer (1994) have shown that exercise in *Cancer productus* can increase cheliped size and strength in subsequent instars. If reduced function in regenerating chelipeds leads to an increased workload for contralateral claws, the latter may become relatively larger and more powerful. Performance levels of regenerating chelipeds and the effect of injury on the contralateral cheliped have not, however, been examined in brachyuran crabs.

Regeneration of a missing appendage involves energetic trade-offs, and cheliped replacement has been shown to reduce size increase at the molt (Bennett, 1973; Chittleborough, 1975; Kuris and Mager, 1975; Hopkins, 1982; Smith, 1990). Because smaller animals are often at a disadvantage in encounters with predators and competitors (Werner and Gilliam, 1984; Garvey et al., 1994), diverting resources meant for growth to regeneration has potentially serious ecological consequences.

In this study, we document the recovery of functional performance in injured *Cancer productus* individuals by comparing the mechanical advantage and maximum crushing force of regenerating claws with the same characteristics in normal claws of injured and intact crabs. We estimate the number of instars required by *C. productus* to regenerate a normal-length cheliped as a function of body size, and we determine the energetic cost of regeneration by comparing growth increments after one molt for regenerating and nonregenerating crabs. Finally, to assess the extent of handicap in *C. productus* populations, we document the frequency of claw loss and regeneration in two populations in Barkley Sound, British Columbia. Our data show that (1) regenerating claws are weaker than the contralateral normal claw, (2) both regenerating and normal claws of injured crabs operate below their size-specific functional capacity, (3) this disadvantage persists for several instars following autotomy, and (4) claw injury is common in the field. As a consequence, the functional cost of autotomy to foraging may be more extensive than previously thought.

Materials and Methods

Claw regeneration and growth increments

Two hundred forty-three crabs ranging in carapace width from 19 to 146 mm were kept between June and August 1993 in laboratory seawater tables at Bamfield Marine Station in Bamfield, British Columbia. Among these were crabs with two normal-size chelipeds (intact) and those missing or regenerating one or both chelipeds (injured). Crabs were held individually in plastic freezer containers (l $\times$ w $\times$ h = 12 cm $\times$ 10 cm $\times$ 13 cm for smaller crabs; 30 cm $\times$ 18 cm $\times$ 10 cm for larger crabs) with mesh sides in constantly flowing seawater (32 ppt salinity, ~12°C temperature). Crabs were fed mussels, *Mytilus californianus* and *M. trossulus, ad libitum* every other day. Each crab received mussels within a size range that it could easily crush.

Cheliped propodus lengths (distance from the proximal end of the manus to the distal tip of the fixed finger) of crabs regenerating one or both chelipeds were measured after each molt to determine percent claw regeneration ([regenerating propodus length/normal propodus length] $\times$100). "Normal" propodus lengths were estimated by regressing carapace width (CW, distance between anterolateral spines, in millimeters) against propodus length for intact crabs with two normal claws (propodus length = 0.456 CW − 2.11, n = 305 chelae, R^2 = 0.98). Mechanical advantage, an indicator of grip strength (Warner and Jones, 1976; Seed and Hughes, 1995), was measured in regenerating and normal claws. Mechanical advantage (L_1/L_2) was calculated by dividing dactyl height (L_1, the distance between the dactyl pivot point and the attachment site of the dactyl with the closer apodeme) by dactyl

length (L_2, the distance between the dactyl pivot point and the dactyl tip) for each claw type. For all crabs that molted while in captivity, we recorded increases in carapace width (in millimeters) and blotted wet weight (in grams) [(postmolt−premolt size)/premolt size] ×100.

Crushing force in regenerating and intact crabs

Crushing forces were determined for regenerating and normal claws of injured crabs and for normal claws of intact crabs by encouraging crabs to grasp a device that registered the force applied. The device consisted of a stationary lower ring and a movable upper ring; the latter was attached at a 90° angle to a 2-mm-thick flexible steel beam by means of a set screw (Smith and Palmer, 1994). Crabs were maneuvered so that the fixed finger of the cheliped fit into the lower ring and the dactyl into the upper ring, each at their midpoint. The distance between the inner margins of the rings was set at about 60% of the maximum gape (determined by regression of maximum gape of normal claws *versus* CW) at the midpoint of the claw. Crabs were held stationary with their chela at a right angle to the rings and allowed to squeeze the rings for 10 s. Forces were transduced by two strain gauges (BAE-13-250BB-350TE: 350 Ω, William Bean, Inc., Detroit, MI) glued to opposite sides of the beam. The signal was amplified by a Wheatstone bridge powered by two 6-V batteries and registered onto a Hewlett-Packard 8045A X-Y chart recorder. Crushing forces (newtons) were calculated after calibrating with known weights.

Crushing force measurements for selected crabs were conducted over a period of 1 month. Crabs were given at least 24 h to recuperate between trials. For crabs with regenerating claws, normal and regenerating claws were measured on alternate trial days. For crabs with two normal claws, right and left claws were tested on alternate trial days. Crabs that molted less than 2 weeks prior to or 1 week subsequent to the tests were excluded from analysis, as were crabs that crushed in less than 50% of the trials (mean number of trials per claw in which crushing occurred ± 1 SD = 4.7 ± 1.6). Because differences in the crab's motivational state produced highly variable crushing forces, only the maximum crushing force for each claw was included in our analyses.

Frequency of autotomy and regeneration

We compared the frequency of cheliped autotomy and regeneration in two populations of *Cancer productus* from Barkley Sound, British Columbia. Crabs were collected by hand at low tide from Grappler Inlet (48° 50′N, 125° 07′W) and Dixon Island (48° 51′N, 125° 07′W) in June 1993. We measured crabs for carapace width and recorded their sex (Dixon Island population only). Crabs were divided into small (CW < 65 mm) and large (CW ≥

65 mm) size classes for analysis. This division roughly corresponded with the onset of sexual maturity in *C. productus* (Orensanz and Gallucci, 1988). Chelipeds were classified either as (1) missing (stump, papilla, or limb bud), (2) regenerating (functional but shorter than normal-length limbs), or (3) normal (full length with no evidence of regeneration).

All statistical analyses were performed using Statistical Analysis Systems software (SAS Institute, 1985).

Results

Claw regeneration rate

Field and laboratory data indicate that *Cancer productus* requires at least three instars to regenerate 100% of the normal, contralateral cheliped length. In the field, the percentage of cheliped length regenerated in large crabs was bimodally distributed with peaks at 60% and 85% the length of a normal cheliped (Fig. 1). Small crabs appeared to regenerate slightly more (70% and 90%) of their normal cheliped length than large crabs over successive molts (Fig. 1). Increases in cheliped length in laboratory-reared crabs mirrored regeneration patterns observed in field populations. In the laboratory, the greatest percent increase (± 1 SD) in limb length (66% ± 11%, $n = 8$) occurred in the first molt following autotomy, when the regenerate expanded from a bud to a short, functional limb. The mean percent increase in limb length over subsequent molts was substantially less (8% ± 7%, $n = 22$). Seven of the individuals with regenerated chelipeds increased less than 4% in cheliped length after the molt. The percentage of cheliped length regenerated in the first post-autotomy molt varied inversely with crab body size (Fig. 2).

Claw performance and mechanical advantage

Recovery of measurable crushing force in regenerating claws required at least two instars following autotomy. In experiments designed to record claw crushing forces, injured crabs (*i.e.*, those with one normal and one regenerating cheliped) exerted measurable crushing force in all trials significantly less often than did crabs with two normal claws ($\chi^2 = 12.3$, df = 2, $P = 0.002$; Table I). Among injured crabs, individuals that had regenerated <75% of a normal cheliped length squeezed the rings significantly less often than crabs that had regenerated ≥75% of a normal cheliped length (Table I). Normal and regenerating claws of injured crabs did not differ in their frequency of successful crushing attempts (Fisher's exact tests, Table I).

Because only two measurable crushing forces were available for injured crabs with <75% of the cheliped length regenerated, we report crushing forces only of
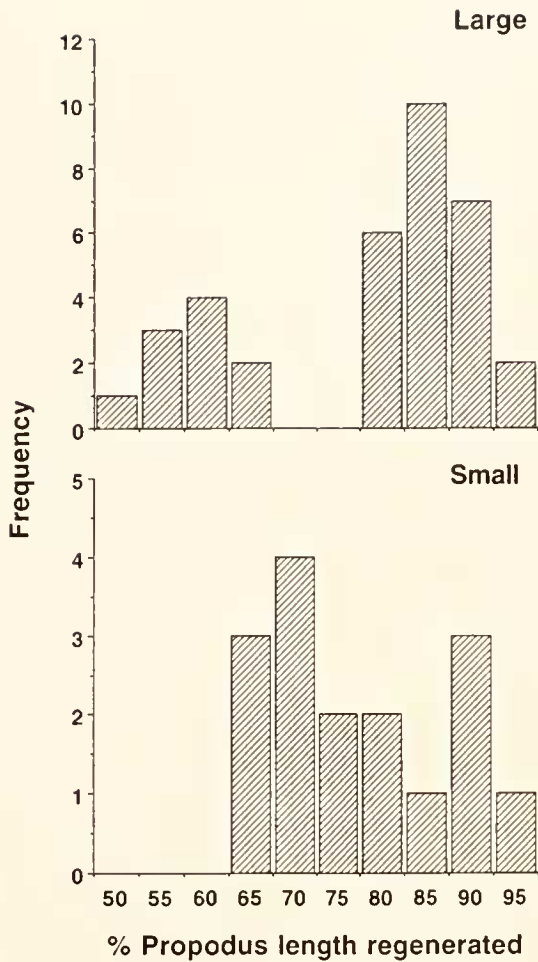
Figure 1. The frequency distribution of percent cheliped length regenerated in small (carapace width [CW] <65 mm) and large (CW ≥ 65 mm) *Cancer productus* individuals collected from Grappler Inlet and Dixon Island. Percent cheliped length regenerated was calculated from propodus length using the equation ([regenerating propodus length/normal propodus length] × 100). Normal propodus lengths were estimated by regressing CW against propodus length for intact crabs with two normal chelipeds.

1981). Crushing force correlated positively with the co-variate, propodus length ($F = 219.6$, df = 1, $P < 0.001$), and slopes of the regression of crushing force *versus* propodus length were homogeneous among claw types (claw type × propodus length interaction, $F = 0.59$, df = 2, 57, $P = 0.56$). Among individuals, least squares mean crushing force was dependent on claw type (one-way ANCOVA, $F = 6.41$, df = 2, $P = 0.003$) (Fig. 3A). Normal claws of intact crabs were significantly stronger than either regenerating ($F = 7.1$, df = 1, $P = 0.010$) or normal ($F = 11.1$, df = 1, $P = 0.0015$) claws of injured crabs (linear contrasts followed by sequential Bonferroni, experimentwise alpha = 0.05; Rice, 1989) (Fig. 3A). For injured crabs, size-adjusted crushing forces of normal and regenerating claws did not differ ($F = 0.14$, df = 1, $P = 0.71$).

Among experimental animals, mechanical advantage did not correlate with the covariate, propodus length ($F = 1.5$, df = 1, $P = 0.23$). Least squares mean mechanical advantage differed among claw types (one-way ANCOVA, $F = 4.0$, df = 2, $P = 0.023$), but did not follow the same pattern as crushing force (Fig. 3B). Instead, size-adjusted mean mechanical advantage (± 1 SE) was highest for normal claws opposite regenerating claws (0.42 ± 0.008) and lowest for regenerating claws (0.38 ± 0.01) (linear contrast, $F = 7.6$, df = 1, $P = 0.008$; Fig.
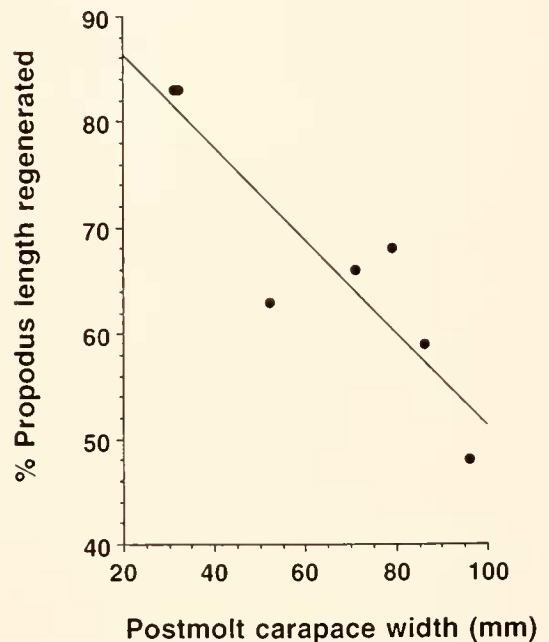
claws that had regenerated more than 75% of the normal claw length. Within these individuals (34 to 98 mm, CW range), the mean crushing force (± 1 SD) of the regenerating claw (23.9 ± 11.3 N) was significantly less than that of the opposing normal-size claw (31.0 ± 15.9 N) (Paired *t* test, $t = 2.84$, $n = 12$, $P = 0.016$). The mean mechanical advantage of the regenerating claw (0.378 ± 0.032) was also less than that of the contralateral normal claw (0.425 ± 0.048) (Paired *t* test, $t = 2.97$, $n = 12$, $P = 0.013$).

We compared crushing forces and mechanical advantages of the different claw types (*i.e.*, normal claws from intact crabs, normal and regenerating claws from injured crabs) after adjusting for propodus length (mean propodus length = 27.1 mm; range, 10 to 42 mm) (Sokal and Rohlf,

Figure 2. Percent propodus length regenerated in first post-autotomy molt of crabs missing one cheliped as a function of carapace width (CW, in mm). Smaller *Cancer productus* individuals regenerate proportionally more than larger individuals (% propodus length regenerated = −0.438 CW + 95.1, $n = 7$, $R^2 = 0.81$, slope SE = 0.0947, $P = 0.006$).

Table I

Comparison of crushing success of intact crabs with normal claws and injured crabs with one normal and one regenerating claw

Crushing success	Intact crabs[a] Two normal claws	Injured crabs, <75% regenerated[b]		Injured crabs, ≥75% regenerated[c]	
		Normal claw	Regenerating claw	Normal claw	Regenerating claw
Yes	25 (83.3%)	2 (22.2%)	0 (0.0%)	9 (42.9%)	10 (47.6%)
No	5 (16.7%)	7 (77.8%)	9 (100.0%)	12 (57.1%)	11 (52.4%)
Fisher's exact test	not applicable	$P = 0.47$		$P = 1.0$	

Injured crabs were subdivided into those individuals with regenerating claws whose propodus lengths were $<$ and $\geq 75\%$ of a normal, contralateral propodus length. Values represent the number (and percentage, in parentheses) of crabs which exerted (Yes) or failed to exert (No) measurable crushing force in all trials (mean number of trials $\pm$ 1 SD = 5.2 $\pm$ 1.4). Different superscripted letters denote significant differences in crushing success of paired claws among different crab categories ($P < 0.05$, STP test; Sokal and Rohlf, 1981). Fisher's exact tests compare normal and regenerating claws within categories of injured crabs.

3B). Size-adjusted mean mechanical advantage of normal claws of intact crabs (0.39 ± 0.008) did not differ from that of regenerating claws of injured crabs ($F = 1.1$, df $= 1$, $P = 0.30$) and was marginally nonsignificant compared to normal claws of injured crabs ($F = 3.6$, df $= 1$, $P = 0.063$) (linear contrasts followed by sequential Bonferroni, experimentwise alpha $= 0.05$).

Among injured crabs collected from Dixon Island and Grappler Inlet, mechanical advantage increased as the cheliped grew through successive regenerative molts (mechanical advantage $= 0.00124\%$ propodus length regenerated $+ 0.267$; $n = 80$, $R^2 = 0.19$, slope SE $= 0.000292$, $P < 0.001$) (Fig. 4). This positive relationship is not simply a function of increasing body size over successive molts, because although mechanical advantage correlated positively with carapace width for regenerating claws ($P = 0.028$), there was no such relationship for normal claws ($P = 0.96$) of injured crabs. Instead, claw dimensions relevant to mechanical advantage are likely changing during regeneration. As evidence, mechanical advantage correlated positively with dactyl height (L_1) of regenerating claws (Pearson correlation coefficient, $r = 0.26$, $n = 80$, $P = 0.017$), but not with dactyl height of normal claws of injured crabs ($r = 0.19$, $n = 78$, $P = 0.10$). Mechanical advantage did not correlate significantly with dactyl length (L_2) of regenerating ($r = 0.016$, $P = 0.89$) or normal ($r = -0.082$, $P = 0.48$) claws of injured crabs.

Growth increments

The energetic cost of cheliped replacement to growth depended on whether one or both claws were regenerating (one-way ANOVA, $F = 6.46$, df $= 3$, $P < 0.001$). Carapace width increments (proportions arcsine-transformed prior to analysis) at the molt did not differ between intact crabs and those regenerating a single cheliped, regardless of whether regeneration began from a limb bud or a partially regenerated limb (Table II). In contrast, regeneration of both claws significantly reduced carapace width increments relative to those of intact or singly injured crabs. Similar trends were observed for wet-weight increments at the molt, but differences among claw conditions were marginally nonsignificant (Kruskal-Wallis test, $\chi^2 = 7.70$, df $= 3$, $P = 0.053$) (Table II).

Frequency of autotomy and regeneration

About one-third of *Cancer productus* individuals collected from Dixon Island (32%; $n = 183$) and Grappler Inlet (29%; $n = 126$) were missing or regenerating one or both chelipeds (two-way logistic regression, site effect, $\chi^2 = 0.03$, df $= 1$, $P = 0.87$; Table III). Large crabs were nearly two times more likely to be injured than small crabs (size effect, $\chi^2 = 17.4$, df $= 1$, $P < 0.001$), and this size dependence was consistent between sites (size $\times$ site interaction, $\chi^2 = 0.38$, df $= 1$, $P = 0.54$; Table III). For combined sizes, the frequency of crabs missing chelipeds did not differ from that of crabs regenerating chelipeds at either site (G-tests, df $= 1$, $P > 0.1$). The majority of injured crabs (97% at Dixon; 86% at Grappler) were missing or regenerating one claw only; loss of both claws was rare (Table III). In the Dixon Island population (data unavailable for Grappler Inlet), right and left chelipeds were missing and regenerating with equal frequency (G-tests, df $= 1$, $P > 0.1$), and the frequency of autotomy was independent of sex ($\chi^2 = 0.40$, df $= 1$, $P = 0.53$; 96 males and 87 females).

Discussion

Foraging costs during claw regeneration

Previous experiments have shown that crabs with missing (Smith and Hines, 1991a) or damaged (Juanes and Hartwick, 1990) claws forage less successfully than do crabs with both claws intact. Our results demonstrate that functional costs persist well into the regenerative process.
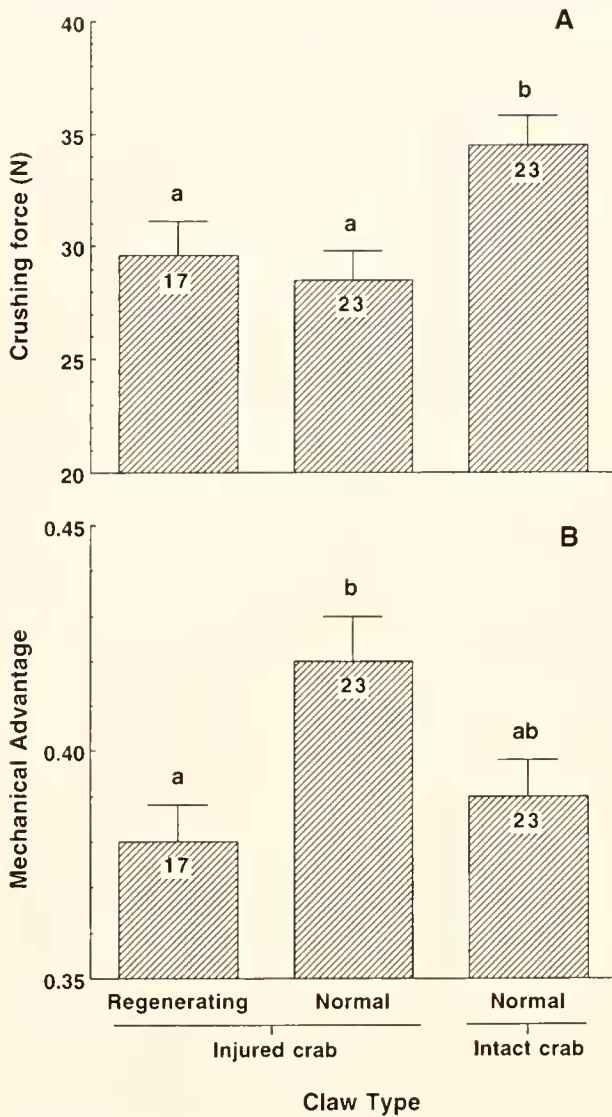
Figure 3. Comparison of (A) crushing force (in newtons) and (B) mechanical advantage of regenerating and normal chelipeds of injured crabs and normal chelipeds of intact crabs. Only regenerating chelipeds with propodus lengths at least 75% of contralateral normal propodus length were included. Crushing forces and mechanical advantages ($\pm$ 1 SE) were adjusted for the covariate, propodus length, using least squares estimation (one-way ANCOVAs; mean propodus length = 27.1 mm) (Sokal and Rohlf, 1981). Mechanical advantage = L_1/L_2; where L_1 is the distance between the dactyl pivot point and the dactyl attachment site with the closer apodeme and L_2 is the distance between the dactyl pivot point and the dactyl tip. Different letters above bars denote means that differ significantly (linear contrasts followed by sequential Bonferroni, experimentwise alpha = 0.05; Rice 1989). Sample size (n) is given for each claw type.

>75% of the normal cheliped length had been regenerated) (Table 1). Even then, regenerating claws exerted significantly less crushing force than did contralateral intact claws. Reduced performance in regenerating claws is not surprising, because crushing force is correlated with claw size (Vermeij, 1977; Elner, 1980; Lee and Seed, 1992; Lee, 1993), and regenerating claws are smaller than their intact counterparts. Regenerating claws should also be constrained to handle smaller prey because of the smaller gape between the fixed and movable fingers. Elner (1980) noted that *Carcinus maenas* males with proportionately smaller chelae (*i.e.,* presumably those with regenerating claws) chose smaller mussel prey and had a lower energy intake per day than did equivalent-size males with normal claws.

Our experiments revealed two less obvious but potentially important effects of autotomy on foraging ability. First, normal claws of injured crabs showed a morphological response to loss of function by the regenerating claw (Fig. 3B). Specifically, we observed a strong trend ($P = 0.063$) toward greater mechanical advantage in the normal claws of injured rather than intact crabs. Second, both normal and regenerating claws in injured crabs operated below their size-specific crushing capacity (Fig. 3A). These results are intriguing, because previous work has
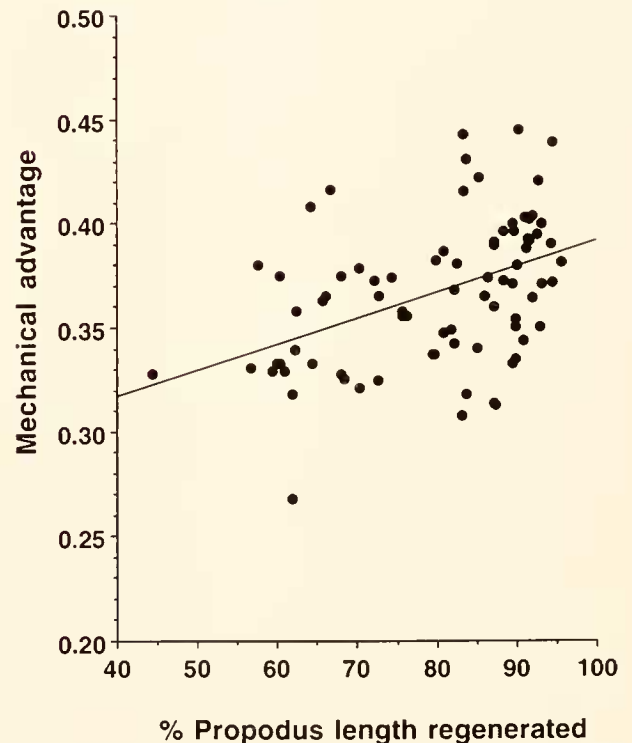
Figure 4. Mechanical advantage as a function of percent propodus length regenerated. Mechanical advantage increases as the cheliped goes through successive regenerative molts ($P < 0.001$, $R^2 = 0.19$).

After the first post-autotomy molt, regenerating claws of *Cancer productus* individuals could not grip forcefully; hence, they would be of little assistance while foraging. Measurable crushing forces were detected in regenerating claws only after the second post-autotomy molt (*i.e.,* when

Table II

Comparison of mean percent carapace width (CW) and wet weight (weight) increments after one molt among crabs with two normal chelipeds and those initially missing or regenerating one cheliped or regenerating two chelipeds

| | Crab cheliped status[1] | | | | | | | | |
| | 2 claws normal | | 1 claw missing 1 claw normal | | 1 claw regenerating 1 claw normal | | 2 claws regenerating | | |
Size category	Mean	n	Mean	n	Mean	n	Mean	n	P
CW[2]	28.7[a] (27.0–30.5)	29	26.4[a] (22.4–30.6)	5	24.9[a] (22.3–27.5)	12	18.1[b] (13.8–23.0)	3	0.001
Weight	98.5 (24.3)	21	99.8 (11.5)	4	87.8 (28.8)	11	56.6 (8.4)	2	0.053

CW (mm) and wet weight (g) increments calculated as [(postmolt − premolt value)/premolt value] × 100. Variances for carapace width increments were homogeneous; those for wet weights were not (F_{max}-tests, alpha = 0.05). For carapace width, mean percent increments, sample sizes (n), 95% confidence intervals (in parentheses), and significance level (P) of the ANOVA are presented. For wet weight, mean percent increments, sample sizes (n), standard deviations (in parentheses), and significance level of Kruskal-Wallis test are presented. Different superscripted letters denote significant differences in carapace width increment among crabs with different degrees of injury (Ryan's Q test; Day and Quinn, 1989).

[1] Missing chelipeds include limb stumps possessing a papilla or limb bud. Regenerating chelipeds have undergone at least one post-autotomy molt, but remain shorter than normal chelipeds.

[2] Means and confidence limits for carapace widths were backtransformed for presentation (arcsine-transformed mean square error = 0.00266, error df = 45, F = 6.5).

shown that *Cancer productus* responded to increased exercise by developing larger and stronger claws in subsequent instars (Smith and Palmer, 1994). Furthermore, if one claw was immobilized, the remaining functional claw became larger and stronger by the next instar (Smith and Palmer, 1994). Given that an injured crab is (1) without a claw for the period immediately following autotomy until the next molt and (2) without a fully functional claw for at least two instars while the appendage regenerates,

the remaining normal claw should be subject to prolonged exercise.

Despite their greater mechanical advantage, normal claws of injured crabs were still relatively weaker than equivalent-size normal claws of intact crabs (Fig. 3A). At least three possible explanations exist for this finding. First, among the size range of mussels presented, injured crabs may have selected smaller mussels than did intact crabs (*e.g.*, Elner, 1980). In crushing smaller prey, both

Table III

Frequencies (n) and percentages (%) of crabs missing and regenerating one or both chelipeds at Dixon Island and Grappler Inlet sites, Barkley Sound, Canada, in June 1993

| | Dixon Island | | | | | | Grappler Inlet | | | | | |
| | Small | | Large | | Total | | Small | | Large | | Total | |
Category	n	%	n	%	n	%	n	%	n	%	n	%
Total intact	73	81.1	51	54.8	124	67.8	63	77.8	26	57.8	89	70.6
Total injured[1]	17	18.9	42	45.2	59	32.2	18	22.2	19	42.2	37	29.4
1 missing	8	8.9	19	20.4	27	14.8	6	7.4	7	15.5	13	10.3
2 missing	1	1.1	0	0.0	1	0.5	1	1.2	1	2.2	2	1.6
1 regenerating	8	8.9	22	23.7	30	16.4	11	13.6	8	17.8	19	15.1
2 regenerating	0	0.0	1	1.1	1	0.5	0	0.0	3	6.7	3	2.4
Total caught	90	100.0	93	100.0	183	100.0	81	100.0	45	100.0	126	100.0

Crabs were divided into two size classes on the basis of carapace width: small = <65 mm; large = ≥65 mm. Values are also given for both size classes combined (Total).

[1] Missing = crabs with scarred stump, papilla, or limb bud. Regenerating = crabs possessing a functional but shortened cheliped. No injured crabs were found missing one cheliped and regenerating the other cheliped.

normal and regenerating claws of injured crabs would receive less exercise than the normal claws of an intact crab, and consequently would remain weaker. We cannot address this question, because systematic records were not kept of the sizes of mussels eaten by injured *versus* intact crabs. Second, unlike the crabs in a study conducted by Smith and Palmer (1994), the crabs in the present experiments were not given mussels whose size was near the upper limit of the crabs' crushing ability; consequently, both the range of exertion needed to forage and the degree of morphological differentiation expressed in the earlier study were greater than in ours. Finally, it is possible that synthesis of new tissue in the regenerating limb might impede extensive muscle development in the contralateral limb. Although a substantial body of work has examined muscle fiber transformation during claw reversal in heterochelous species (*e.g.*, Mellon and Stephens, 1980; Quigley and Mellon, 1986; Govind *et al.*, 1987), there is a dearth of information concerning the influence of regeneration on muscle development in claws of homochelous species such as *Cancer*.

Given the high frequency of claw loss in these (Table III) and other populations of molluscivorous crabs (see review by Juanes and Smith, 1995), a compensatory morphological response by normal claws of injured crabs would be advantageous. The response, however, probably only partially offsets the functional loss of a cheliped. As a consequence, crabs with a regenerating claw should be expected to (1) require longer handling times to subdue hard-shelled prey, (2) modify their tactics for gaining entry to hard-shelled prey, or (3) modify their diet to include smaller or less well defended prey items. Shell-opening tactics in crustaceans are complex (Lau, 1987), and it is possible that behavioral adjustments may compensate for limited crushing power (Hughes and Seed, 1981; Cunningham and Hughes, 1984; Smith and Hines, 1991a; Seed and Hughes, 1995). Direct comparisons of foraging behavior, handling times, and prey choice between injured and intact crabs are needed to determine the true costs of autotomy and regeneration to foraging performance.

Morphological changes during regeneration

As chelipeds regenerate, they become more efficient and forceful foraging tools, in part because of changes in their leverage properties. Mechanical advantage increased as the cheliped regenerated (Fig. 4), primarily because L_1 (the distance between the dactyl pivot point and the attachment site of the dactyl with the closer apodeme) increased faster than L_2 (the distance between the dactyl pivot point and the dactyl tip). L_1 approximates chela height, and Lee (1993) has shown that chela height is a good estimator of claw strength within species. The

allometric change observed in the lever arms was specific to claw regeneration; no such change was observed during the growth of normal claws of injured crabs. The change in mechanical advantage during claw regeneration may reflect a use-induced increase in the underlying muscle as the claw becomes larger and more functional with each molt, or other, as yet unknown, developmental phenomena.

Regeneration time

The length of time required to regenerate a missing limb to normal size can vary dramatically between life-history stages and species of crabs (Juanes and Smith, 1995). Certainly, disadvantages arising from cheliped loss will be lessened if regeneration of the missing appendage(s) is rapid. Both field and laboratory data indicated that *Cancer productus* individuals were able to replace a full-length cheliped in about three molts. The number of instars needed for complete regeneration in *C. productus* thus falls within the range observed for other crab species—for example, two instars for juvenile *Callinectes sapidus* (Smith, 1990); four to seven instars for *Paralithodes camtschatica* (Edwards, 1972). *C. productus* undergoes about 13 molts over 3 years with the ninth (puberty) molt occurring 10 to 11 months after settlement (Orensanz and Gallucci, 1988). If this molting schedule holds for regenerating crabs, then juvenile crabs could recover claws in as little as 2 to 3 months. In contrast, adults could require years. Given that some individuals in our experiments showed almost no size increase (<4%) in their claws after the initial post-autotomy molt, it is possible that some *C. productus* individuals never recover a full-length claw.

It is interesting that in *Cancer productus* and in other crab species (*e.g.*, Skinner and Graham, 1972), individuals regenerate more than half the length of a normal claw in the first molt, but fail to complete the task in the next molt. This phenomenon of rapid, but incomplete, replacement of a missing appendage followed by slower subsequent growth is not confined to crustaceans. For example, Fielman *et al.* (1991) suggested that ophiuroids regenerate lost disc and arm tissue until a "minimal functional configuration" is achieved, then regeneration rates slow. Indeed, selection pressures may be great for replacing the majority of the skeletal framework quickly so that injured animals can "make do." Beyond this, pressure for complete recovery of function diminishes. Energetic resources can then be shunted to other tasks such as growth or reproduction. This scenario may also explain why the proportion of cheliped length regenerated decreased with increased body size in *C. productus* (Figs. 1, 2). If larger crabs are able to forage on a greater range of prey sizes and are at less risk of predation than smaller individuals,

selection for rapid replacement of a missing cheliped may be less intense than for smaller crabs.

Energetic costs to regeneration

Energetic costs, in the form of smaller growth increments at the molt, were seen only in cases of multiple autotomy (Table II). A similar, additive effect of limb loss on growth increment has been observed in other crab species (*e.g.*, Bennett, 1973; Kuris and Mager, 1975; Hopkins, 1982; Smith, 1990). We detected reduced growth increments, though, in crabs that had already undergone one post-autotomy molt. The energetic cost of replacing both chelipeds thus persists well into the regenerative process for *Cancer productus*. It should be noted that in most studies examining the effect of limb regeneration on growth, injured crabs were fed *ad libitum*. In field situations, reduced foraging performance in injured crabs could magnify energetic costs of limb replacement.

Injury frequency in the population

If cheliped loss is high in crab populations, and if foraging ability is compromised for injured crabs under field conditions, then predator-prey dynamics and community structure may be profoundly affected. We observed high frequencies of cheliped damage in *Cancer productus* populations in Barkley Sound: up to 45% of the larger and 22% of the smaller crabs were missing or regenerating a single claw (Table III). A substantial component of the *Cancer productus* population, then, may have to switch to smaller size classes or different types of prey. Injured crabs, in turn, may become more vulnerable to their own predators, if search or handling times increase. The fact that we found few crabs missing or regenerating both chelipeds ($\leq4\%$) suggests that, at the least, multiple autotomy places individuals at a selective disadvantage. Our data suggest that the consequences of claw autotomy for the individual crab are prolonged. The direct and indirect effects of reduced foraging performance in injured crabs on community dynamics remain to be explored.

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